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BULLETIN OF Mathematical Biophysics

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VOLUME ONE

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A COMPARISON OF ELECTRICAL AND DIFFUSION FORCES IN THE METABOLISM OF ELECTROLYTES

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Using an approximation method the electrical forces due to the metabolism of electrolytes have been compared to the ordinary diffusion forces and found negligible.

In the development of mathematical biophysics it has been assumed for the purposes of simplification that electrical forces, created by a difference in the diffusion rates of positive and negative ions produced or consumed in metabolic reaction, would have a negligible effect on the concentration gradients of those ions. Preliminary considerations led N. Rashevsky to believe this to be true. By way of a preliminary study he considered the case of a spherical cell in which the diffusion coefficients are infinite, and only the permeabilities finite (Rashevsky, 1938, p. 126, hereinafter referred to as M.B.). In an earlier paper (Rashevsky, 1935) he discussed the equations for the case of the consumption of two monovalent ions of opposite charge, present in equal quantities at an infinite distance from the cell in which they are consumed. Because of the difficulties in solving these equations the problem has awaited quantitative treatment by a new approximation method (M.B. Appendix).

In this paper we shall apply an approximation method to the case of a spherical cell metabolizing to produce monovalent ions of opposite charge, which ions have different molecular weights and internal diffusion coefficients but infinite permeabilities. Later we shall consider the cases where the permeabilities and external diffusion coefficients are finite and the cell is non-spherical.

In reasonably dilute solutions, where no forces other than those produced by random molecular collisions are considered, Fick's law may be held to apply to the diffusion of metabolites. When, however, a field of force acting on the particles is present we must use a more general formulation of the diffusion problem.

Let

- D = diffusion coefficient of an ion in $\text{cm}^2 \text{sec}^{-1}$,
 c = concentration of an ion in gm cm^{-3} ,
 B = mobility of an ion in sec gm^{-1} ,
 f = force on an ion in dynes,
 k = Boltzmann constant = 1.4×10^{-16} erg. degree $^{-1}$,
 T = absolute temperature,
 J = rate of transport of an ion through the membrane
in $\text{gm cm}^{-2} \text{sec}^{-1}$,
 q = rate of production of an ion in $\text{gm cm}^{-3} \text{sec}^{-1}$,
 M = molecular weight of an ion,
 N = Avogadro's number,
 ε = charge on an electron in E.S.U.,
 E = net charge on the cell in E.S.U.,
 K = dielectric constant of the internal medium,
 V = volume of the cell in cm^3 ,
 r_0 = radius of the cell in cm,

and let the subscripts $+$ and $-$ denote the ions to which the constant applies. Let a bar indicate "average," and the subscript 0 "external" when applied to c .

Then we may write immediately the following relations:

$$B = \frac{D}{kT}; \quad (1)$$

$$J = -D \text{grad } c + Bfc; \quad (2)$$

$$\frac{q_+}{M_+} = \frac{q_-}{M_-}, \quad \frac{c_{0+}}{M_+} = \frac{c_{0-}}{M_-}, \quad f_+ = -f_-. \quad (3)$$

If we consider that $c = \bar{c}$ approximately at $r_0/2$, then approximately

$$-D \text{grad } c = +2D \frac{\bar{c} - c_0}{r_0}. \quad (4)$$

The total charges of the positive and negative ions considered separately are

$$\frac{\bar{c}_+}{M_+} N \varepsilon V \text{ and } \frac{\bar{c}_-}{M_-} N \varepsilon V,$$

so that we may write the net charge on the cell as

$$E = \frac{4}{3} \pi r_0^3 \left(\frac{\bar{c}_+}{M_+} - \frac{\bar{c}_-}{M_-} \right) N \varepsilon. \quad (5)$$

The force on a positive ion at r_0 is

$$f_+ = \frac{E \varepsilon}{K r_0^2} = \frac{4 \pi r_0 N \varepsilon^2}{3K} \left(\frac{\bar{c}_+}{M_+} - \frac{\bar{c}_-}{M_-} \right). \quad (6)$$

Then from equations (2), (4), and (6),

$$J_+ = 2D_+ \frac{\bar{c}_+ - c_{0+}}{r_0} + \frac{4 \pi r_0 N \varepsilon^2 B_+}{3K} \left(\frac{\bar{c}_+}{M_+} - \frac{\bar{c}_-}{M_-} \right) \bar{c}_+; \quad (7)$$

$$J_- = 2D_- \frac{\bar{c}_- - c_{0-}}{r_0} - \frac{4 \pi r_0 N \varepsilon^2 B_-}{3K} \left(\frac{\bar{c}_+}{M_+} - \frac{\bar{c}_-}{M_-} \right) \bar{c}_-.$$

The total transports and productions are

$$4 \pi r_0^2 J_+, \quad 4 \pi r_0^2 J_- \quad \text{and} \quad 4/3 \pi r_0^3 q_+, \quad 4/3 \pi r_0^3 q_-. \quad (8)$$

From considerations of a material balance in the stationary state, and from equations (7) and (8) we have, after rearranging

$$\begin{aligned} 4 \pi r_0^2 \frac{N \varepsilon^2 D_+}{K k T M_+} \bar{c}_+^2 - 4 \pi r_0^2 \frac{N \varepsilon^2 D_+}{K k T M_-} \bar{c}_+ \bar{c}_- \\ + 6D_+ \bar{c}_+ - r_0^2 q_+ - 6D_+ c_{0+} = 0; \\ 4 \pi r_0^2 \frac{N \varepsilon^2 D_-}{K k T M_-} \bar{c}_-^2 - 4 \pi r_0^2 \frac{N \varepsilon^2 D_-}{K k T M_+} \bar{c}_+ \bar{c}_- \\ + 6D_- \bar{c}_- - r_0^2 q_- - 6D_- c_{0-} = 0. \end{aligned}$$

Let $4 \pi r_0^2 \frac{N \varepsilon^2}{K k T} = \rho$ and, assuming $K = 80$ and $r_0 = 10^{-3} \text{ cm.}$, we have $\rho = 4.735 \cdot 10^{12}$. Then dividing the first of these equations by $\bar{c}_+ \rho D_+/M_-$ and the second by $\bar{c}_- \rho D_-/M_+$ gives

$$\bar{c}_- = \frac{M_-}{M_+} \bar{c}_+ + \frac{6M_-}{\rho} - \frac{6M_-}{\rho \bar{c}_+} \left(\frac{q_+ r_0^2}{6D_+} + c_{0+} \right); \quad (a) \quad (9)$$

$$\bar{c}_+ = \frac{M_+}{M_-} \bar{c}_- + \frac{6M_+}{\rho} - \frac{6M_+}{\rho \bar{c}_-} \left(\frac{q_- r_0^2}{6D_-} + c_{0-} \right). \quad (b)$$

Introducing (9a) into (9b) and solving for \bar{c}_+ we obtain after rearranging

$$\begin{aligned}
 0 = \bar{c}_+^3 + & \left[\frac{6M_+}{\rho} - \frac{(q_+ r_0^2)/6D_+ + c_{0+}}{2} - \right. \\
 & \left. \frac{M_+}{2M_-} \left(\frac{q_- r_0^2}{6D_-} + c_{0-} \right) \right] \bar{c}_+^2 \\
 & - \frac{9M_-}{\rho} \left(\frac{q_+ r_0^2}{6D_+} + c_{0+} \right) \bar{c}_+ \\
 & + \frac{3M_+}{\rho} \left(\frac{q_+ r_0^2}{6D_+} + c_{0+} \right)^2.
 \end{aligned} \tag{10}$$

Since the linear and constant terms in \bar{c}_+ contain the factor 10^{-12} but in all other respects are similar to the square term coefficient, they will be negligible with respect to it. Then we have, after dropping them,

$$\bar{c}_+ = \frac{M_+}{2M_-} \left(\frac{q_- r_0^2}{6D_-} + c_{0-} \right) + \frac{1}{2} \left(\frac{q_+ r_0^2}{6D_+} + c_{0+} \right) - \frac{6M_+}{\rho};$$

or since

$$\frac{1}{2} \left(\frac{q_+ r_0^2}{6D_+} + c_{0+} \right) \approx \frac{M_+}{2M_-} \left(\frac{q_- r_0^2}{6D_-} + c_{0-} \right) \gg \frac{6M_+}{\rho},$$

we have

$$\bar{c}_+ = M_+ \left(\frac{q_- r_0^2}{12M_- D_-} + \frac{q_+ r_0^2}{12M_+ D_+} + \frac{c_{0+}}{2M_+} + \frac{c_{0-}}{2M_-} \right).$$

By means of equation (3) this may be written as

$$\bar{c}_+ = M_+ \left(\frac{D_+ + D_-}{D_+ D_-} \frac{q_+ r_0^2}{12M_+} + \frac{c_{0+}}{M_+} \right)$$

or simply

$$\bar{c}_+ = \frac{q_+ r_0^2}{12} \cdot \frac{D_+ + D_-}{D_+ D_-} + c_{0+}; \tag{11}$$

and similarly for \bar{c}_-

$$\bar{c}_- = \frac{q_- r_0^2}{12} \cdot \frac{D_+ + D_-}{D_+ D_-} + c_{0-}. \tag{12}$$

Here we may note the similarity of these equations to those of the diffusion of one substance as derived by the approximation method (M. B. Appendix). When $D_+ \gg D_-$, \bar{c}_+ is proportional to \bar{c}_- and to $1/D_-$, and when $D_- \gg D_+$, \bar{c}_+ is proportional to \bar{c}_- and to $1/D_+$. When (11) and (12) are introduced into (5) we get

$$\frac{4}{3} \pi r_0^3 \left[\frac{D_+ + D_-}{D_+ D_-} \cdot \frac{q_+}{M_+} \cdot \frac{r_0^2}{12} - \frac{D_+ + D_- r_0^2}{D_+ D_-} \cdot \frac{q_-}{12} \cdot \frac{q_-}{M_-} + \frac{c_{0+}}{M_+} - \frac{c_{0-}}{M_-} \right] N \varepsilon = E,$$

and introducing (3)

$$E = 0,$$

and the force vanishes with vanishing charge.

If in equation (10) we let

$$-a = \bar{c}_+^2 \text{ coefficient,}$$

$$b = \bar{c}_+ \quad \text{''},$$

$$c = \text{constant term,}$$

$$x = \bar{c}_+,$$

$$x_0 = a,$$

then we may put:

$$x = x_0 + \Delta,$$

where Δ is a small quantity. Then $x^3 - ax^2 = -(bx + c)$.

In taking $x = a$ we have assumed $-(bx + c)$ to be negligible. If we differentiate $x^3 - ax^2$ at $x = a = x_0$, we get $(3x_0^2 - 2ax_0) \Delta x$, and to obtain a solution of equation (10) more exact than that given by (11) we must set this increment equal to $-(bx + c) = -ab - b \Delta - c$. $(3x_0^2 - 2ax_0) \Delta = (3a^2 - 2a^2) \Delta = a^2 \Delta = -ab - b \Delta - c$.

$$\Delta = -\frac{ab + c}{a^2 + b}.$$

For

$$M_+ = 1;$$

$$D_+ = 10^{-7};$$

$$q_+ = 10^{-5};$$

$$r_0 = 10^{-3};$$

$$\bar{c}_{0+} = 10^{-5};$$

$$M_- = 10^2;$$

$$D_- = 10^{-9};$$

$$q_- = 10^{-7};$$

$$\rho = 4.73 \cdot 10^{12};$$

$$\bar{c}_{0-} = 10^{-7};$$

and

$$a = 1.35 \cdot 10^{-5},$$

$$b = -5 \cdot 10^{-15},$$

$$c = 4.5 \cdot 10^{-22},$$

then $\Delta_+ = -4 \cdot 10^{-10}$ approximately.

For the negative ions

$$\begin{aligned} a &= 1.35 \cdot 10^{-3} , \\ b &= -3 \cdot 10^{-17} , \\ c &= 2 \cdot 10^{-20} , \end{aligned}$$

and $\Delta_- = 1 \cdot 10^{-14}$ approximately.

E is then equal to

$$\frac{4}{3} \pi r_0^3 N \varepsilon \left[\frac{\Delta_+}{M_+} - \frac{\Delta_-}{M_-} \right] ,$$

or about $4.8 \cdot 10^{-4}$ *E.S.U.* on the whole cell. This is sufficient to account for the observed charges on a cell (M.B., p. 126) yet it can be seen that it does not affect the diffusion gradients within the limits of experimental error.

We may conclude therefore, that in a spherical cell the accumulation of a charge on a cell by selection of ions of different charge through different diffusion rates does not materially affect diffusion gradients or forces. We have also shown that an appreciable charge can be produced by metabolism using reasonable values of the constants of a cell. This may account for the charges that vanish with death of the cell as contrasted with charges produced by a Donnan equilibrium in the membrane, which would not vanish at death.

In the special case just considered where $h = D_e = \infty$, the molar concentrations of the ions are identical at the surface, and since only average (linear) gradients are considered, any differences in molar concentrations will have the same sign throughout the cell; i.e., either $c_+/M_+ \geq c_-/M_-$ for every $r \leq r_0$ or $c_+/M_+ \leq c_-/M_-$. On the other hand, if D_e and (or) h are finite, the molar concentrations need not be the same at the surface, and $c_+/M_+ \geq c_-/M_-$, depending on r . This could produce a change in sign of the local charges as different regions are considered. The average charge may then be very small, but large local charges may exist which might create local forces of importance (in nuclear division, mitosis, protoplasmic streaming, or nerve excitation and conduction). Since these effects are of a purely local nature and since in the work that has been done previously (Young, 1939; Rashevsky, 1939) only average gradients, concentrations, and forces have been considered, the possibility of strong localized effects does not in any way affect the work of the past. The gross features of cellular mechanics will remain unchanged, and such considerations of local electrical forces need be made only when considering phenomena of a localized nature. The possible application of these local forces to such phenomena as nerve excitation and conduction will be discussed in the future.

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A CONTRIBUTION TO THE MATHEMATICAL BIOPHYSICS OF PSYCHOPHYSICAL DISCRIMINATION II

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The properties of a neural mechanism previously discussed are given in more general form. It is shown that, under certain conditions, a psychophysical scale value is proportional to a difference between excitation factors at a synapse. More general relations are derived which hold among different variables in the two and three categories of judgment. An attempt is made to apply the results to the method of choices. Certain relations derived are compared with available experimental data.

I

In a previous paper (Landahl, 1938) the properties of a neural mechanism for discrimination were developed in analytic form by the use of an arbitrary distribution function of the fluctuation of excitation at a synapse. Let us now discuss certain properties without specifying the distribution function. By so doing, it may be possible, to some extent, to correlate the results with some phases of psychophysics. The results are then immediately extended. If any new relations are suggested in the process, it is so much the more fortunate. We confine our interest, however, to those situations in which it is possible, at least in principle, to obtain restrictive conditions upon the basic nerve parameters (Rashevsky, 1938, Ch. XXII) from experimental data.

If $(\varepsilon - j)'$ is the value of the next excitation at s_2^* (Landahl, 1938, Figure 1) due to random factors, we then have $p(\varepsilon - j)' d(\varepsilon - j)'$ as the probability that the random fluctuation, $(\varepsilon - j)'$, has a net excitation (stimulus) value which lies between $(\varepsilon - j)'$ and $(\varepsilon - j)' + d(\varepsilon - j)'$. As in the previous development [Landahl, 1938, equation (9)] we obtain for the probability of a wrong response, P_w , when the two stimuli are presented, and only a correct or a wrong response is allowed,

* The following applies, irrespective of the symmetry of the function p , if we transfer the fluctuation to synapse s_2 . The transfer eliminates the use of $P(-x)$ [equation (2)], which if symmetry is assumed, equals $1 - P(x)$.

$$P_w = \int_{\varepsilon_1 - \varepsilon_2}^{\infty} p(\varepsilon - j)' d(\varepsilon - j)' \quad (1)$$

which, for the distribution used previously [Landahl, 1938, equation (7)] reduces to the former expression [Landahl, 1938, equation (10)]. However, if we do not specify the function p , equation (1) together with the definition of equation (2),

$$P(x) = \int_{-\infty}^x p(\varepsilon - j)' d(\varepsilon - j)' \quad (2)$$

becomes

$$P_w = \int_{\varepsilon_1 - \varepsilon_2}^{\infty} p d(\varepsilon - j)' = \int_{-\infty}^{\infty} p d(\varepsilon - j)' - \int_{-\infty}^{\varepsilon_1 - \varepsilon_2} p d(\varepsilon - j)'$$

or

$$P_w = 1 - P(\varepsilon_1 - \varepsilon_2) . \quad (3)$$

The probability for a correct response is then

$$P_c = P(\varepsilon_1 - \varepsilon_2) . \quad (4)$$

Using the relations I, II, III [Landahl, 1938, p. 115], we may write for P'_w , the probability of a wrong response, P'_d , the probability of an equality response and P'_c , the probability of a correct response, (the primes referring to the case in which the intermediate category is allowed) the following relations:

$$P'_w = \int_{(\varepsilon_1 - \varepsilon_2 + h)}^{\infty} p d(\varepsilon - j)' = 1 - P(\varepsilon_1 - \varepsilon_2 + h) , \quad (5)$$

$$P'_d = \int_{(\varepsilon_1 - \varepsilon_2 - h)}^{(\varepsilon_1 - \varepsilon_2 + h)} p d(\varepsilon - j)' = P(\varepsilon_1 - \varepsilon_2 + h) - P(\varepsilon_1 - \varepsilon_2 - h) , \quad (6)$$

$$P'_c = \int_{-\infty}^{(\varepsilon_1 - \varepsilon_2 - h)} p d(\varepsilon - j)' = P(\varepsilon_1 - \varepsilon_2 - h) . \quad (7)$$

The value of $\varepsilon_1 - \varepsilon_2$, for the particular $E(S)$ relation and $p(\varepsilon - j)'$ relation previously used, is given by [Landahl, 1938, equation (5)]

$$\varepsilon_1 - \varepsilon_2 = L \log \frac{S_1}{S_2} \doteq L \frac{S_1 - S_2}{S_2} , \quad (8)$$

where

$$L = \frac{AK}{a} (1 - e^{-at}) \quad (9)$$

and A, K and a are nerve constants, t is the time and S_1 , and S_2 are the stimulus magnitudes, $S_1 > S_2$. The second approximate relation

of (8) holds when S_1 and S_2 are fairly nearly equal and is obtained by taking first order terms in the expansions. According to the approximation one would be justified in plotting the P 's against per cent differences in the stimuli compared.

If we now let one of the stimuli be the standard and permit the other to be larger than, equal to, or smaller than the standard, and let the subscripts g , d , and l mean "greater", "doubtful" ("equal"), and "smaller", we have $P'_d = P'_d$ and

$$P'_g = P'_c, P_g = P_c, P'_l = P'_w, P_l = P_w \text{ for } S \geq S_s,$$

S being compared with the standard S_s , and

$$P'_g = P'_w, P_g = P_w, P'_l = P'_c, P_l = P_c \text{ for } S \leq S_s.$$

Then introducing

$$x = L \log \frac{S}{S_s} \doteq L \frac{S - S_s}{S_s}, \quad (10)$$

we may write the relations

$$P_l = 1 - P(x), \quad (11)$$

$$P_g = P(x), \quad (12)$$

$$P'_l = 1 - P(x + h), \quad (13)$$

$$P'_d = P(x + h) - P(x - h), \quad (14)$$

$$P'_g = P(x - h), \quad (15)$$

where now $-\infty < x < \infty$. From equation (9), x is a function of the time t , and the time relations are the same as previously discussed (Landahl, 1938).

In deriving the above relations it has been assumed that the mechanism was symmetric. Then if $P(x) \neq \frac{1}{2}$ for $x = 0$, so that a constant error (Culler, 1926, pp. 56-62; Guilford, 1936, pp. 27-29) is present, it is due either to a displacement of the distribution function or the fact that it may not be symmetric. Now if we assume that the function p is symmetric with a maximum at $x = 0$, but that the mechanism (Landahl, 1938, Figure 1) is not, we have for the difference $\varepsilon_1 - \varepsilon_2$, instead of equation (8), the expression

$$\begin{aligned} \varepsilon_1 - \varepsilon_2 = & \frac{A_1 K_1}{a_1} (1 - e^{-a_1 t}) \log \frac{S_1}{h_{01}} \\ & - \frac{A_2 K_2}{a_2} (1 - e^{-a_2 t}) \log \frac{S_2}{h_{02}}. \end{aligned} \quad (16)$$

Introducing S , S_s , and x , equation (16) may be written

$$x = \frac{A_2 K_2}{a_2} \left[\log \frac{S^\gamma}{h_{01}^\gamma} - \log \frac{S_s}{h_{02}} \right] (1 - e^{-a_2 t}), \quad (17)$$

or

$$x = L_2 \log \frac{S^\gamma}{S_s} - x'_0 = L_2 \frac{S^\gamma - S_s}{S_s} - x'_0 \quad (18)$$

where

$$\gamma = \frac{A_1 K_1 a_2 (1 - e^{-a_1 t})}{A_2 K_2 a_1 (1 - e^{-a_2 t})}, \quad (19)$$

$$x'_0 = L_2 \log \frac{h_{01}^\gamma}{h_{02}}. \quad (20)$$

We may then have a shift in the point of subjective equality or in the constant error due to asymmetry in the function p and also due to the asymmetry in the neural mechanism, $h_{01} \neq h_{02}$; and the latter shift may change with time.

If the thresholds of synapses s_1 and s_2 are not equal [or similarly for s_3 and s_4 (Landahl, 1938, p. 109)] the resulting bias is equivalent to a shift in the maximum of the distribution function by an amount equal to the difference in the thresholds. Such an asymmetry in the mechanism would be a most plausible cause of the displacement of the maximum of p from $x = 0$. This type of bias might be termed a response bias as against a bias due to a difference in threshold of a sensory apparatus, $h_{01} \neq h_{02}$. Consider, for instance, the case in which the left eye views the left stimulus and the right eye views the right. Let the left-right response bias, as discussed above, be eliminated. A bias might then be present due to a difference in sensitivity of the eyes, $h_{01} \neq h_{02}$, or to a difference in the parameters $\left[\frac{AK}{a} \right]$ of equation

(16) of the nerve tract fibers (Landahl, 1938, Fig. 1, I and II). A measurable change in the bias might be obtained as a result of a one-sided change in the illumination conditions, introduction of color, the application of drugs affecting the pupil, the neural elements of the retina and the optic tract, etc. The information so obtained should be compatible with the present concepts of the parameters involved.

We are discussing here only the case in which the stimuli being compared are presented simultaneously. If the stimuli are not presented simultaneously, on the basis of the mechanism under consideration, the second stimulus would be very much favored. If the stimuli are not maintained together sufficiently long, no discrimination is possible. However, by the addition of another mechanism to be discussed in a subsequent paper these temporal effects are changed.

Let us now make the results more general by introducing an uni-

specified relation $\varepsilon(S)$ between ε , the value of the excitation factor at a higher center (as s_1 or s_2), and S , the external stimulus magnitude. Following an argument similar to that above, we obtain equations identical to equations (11) to (15) but with x defined by

$$x = \varepsilon(S) - \varepsilon(S_s), \quad (21)$$

instead of by equation (10), S being the stimulus which is compared with the standard S_s .

The probability P_g of a response S greater than S_s is, according to equation (12), equal to $P(x)$, where x is given by (21). The proportion of responses of S greater than S_s may be determined empirically under given conditions and, if the conditions are suitable, we may assume that the proportion will equal the value of the probability, $P(x)$. Then, since $P(x)$ is known, if the distribution function, p , is known, or may be assumed to be Gaussian, x is determined in terms of some unknown unit. As long as the unit cannot be determined in terms of the synaptic threshold h_1 , (x and ε have the same dimension as the threshold), it might well be expressed as a standard deviation unit according to the customary methods of scaling (Guilford, 1936, p. 216). Under these conditions, a scale value is proportional to a difference between two excitation factors at the discriminating center.

II

Let us now discuss the relations (11) to (15) in connection with available experimental data. We first shall discuss the data by F. M. Urban on lifted weights (Urban, 1908). Seven subjects were asked to judge seven weights with respect to identical standards 300 or 450 times each and the judgments allowed were "heavier", "guess heavier", "guess lighter", and "lighter." The "equality" or "doubtful" category was taken as the "guess heavier" plus "guess lighter" judgments.*

If we identify the various proportions experimentally derived with the respective probabilities, and if we assume that the probability distribution function is Gaussian, or

$$p(\varepsilon - j)' = \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{[(\varepsilon - j)' - x_0]^2}{2\sigma^2}}, \quad (22)$$

* In Urban's notation the symbols used were respectively h , hg , lg , and l , with $T = hg + lg$. Then in transferring to the notation used above we have $h = P_g'$, $h + hg = P_g$, $l = P_l'$, $l + lg = P_l$, and $T = P_d'$. The change in notation is made so as to have a consistent notation for all the experiments discussed and in order not to conflict with the notation previously adopted.

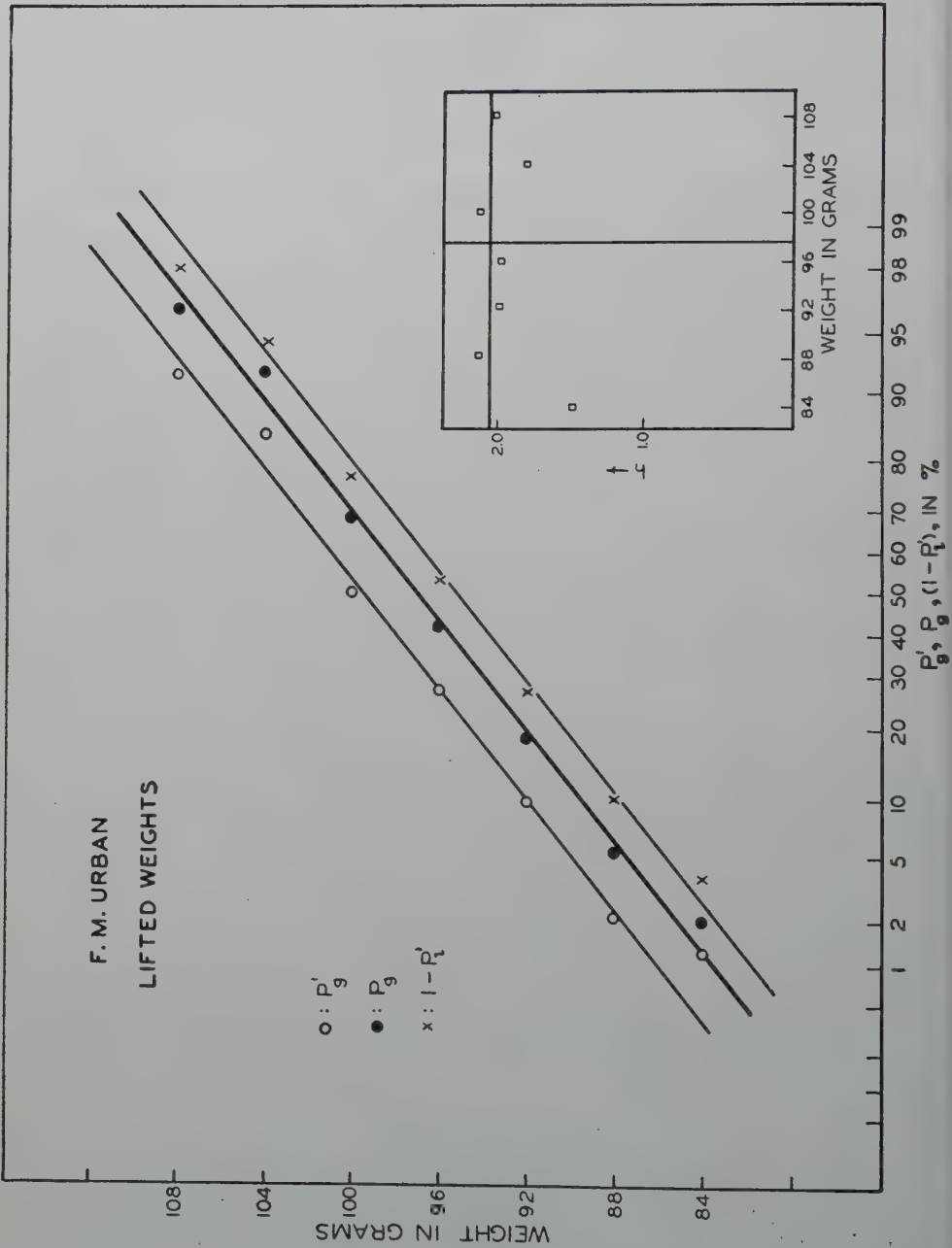


FIGURE 1

then from equations (15), (12) and (14), P'_g , P_g and $P'_g + P'_d$ are normal cumulative frequency curves. In order to show the agreement with experiment in a most sensitive manner the experimental points are plotted on an arithmetic probability scale, on which the points should then fall along three parallel straight lines. This holds since the differences $S - S_s$ are small compared with S_s , and from equation (10), x is very nearly linear with $S - S_s$.

In Figure 1 the averaged results from seven subjects are plotted on arithmetic probability paper. The results indicate essentially three parallel straight lines. The individual plots are similar to the average in this respect. The centrally located data, P_g are slightly displaced toward the right of an exact central position. If this is taken as significant here, as it definitely is for individual cases, the interpretation on the basis of the mechanism is that the rise in threshold h for the three category case is not the same at s_3 and s_4 (Landahl, 1938, Fig. 1). Such a bias does not seem unnatural. The result is the same as if there were a shift in the mean of the distribution function from the two to the three category case. The standard deviation of the distribution functions, σ , was taken as 5.7 grams. The mean for the two category case was taken as 97.1 grams and for the three category case, 97.4 grams. The standard stimuli weighed 100 grams. The value of h was taken as 2.1 grams. Here, as elsewhere, we take the value of x as if it were given in the physical units of intensity. Strictly, from equation (10) we should involve the coefficient L . However, the unit of x is still not known so, for simplicity, we refer to x as if measured in grams, etc.

On examining the visual and auditory data (Kellogg, 1930), we find somewhat more complex results. Before discussing the data, let us more specifically examine the meaning of the two and three category cases on the basis of the mechanism under consideration. We shall assume that generally $h \neq 0$ in equations (13), (14) and (15) so that the three category case is the more general situation. Now when the two category case is required, h must necessarily be zero when the judgment is given and hence we shall assume that the stimulus "two category" or its equivalent leads, through some center, C , to an excitation at s_3 and s_4 (Landahl, 1938, Fig. 1) which reduces the threshold to zero.

It might be that even in the three category case there may be a tendency for the stimuli to influence the center, C , which lowers the threshold of s_3 and s_4 . This would happen if excitatory fibers from s_3 and s_4 (Landahl, 1938, Fig. 1) lead to C . Then, if the parameters a of the fibers leading to and from C are large compared with those of the other fibers of the mechanism, and if their thresholds are

negligible, the increase in excitation at s_3 and s_4 , or decrease in h , is a function of $\varepsilon_3 - j_4$ (Landahl, 1938, Fig. 1). Now $\varepsilon_3 - j_4$ is a monotonically increasing function of ε_1 and ε_2 and in the steady state, the two quantities are proportional. With a proper choice of the nerve parameters, $A/a = B/b = 1$ (Rashevsky, 1938, Ch. XXII), we may make the constant of proportionality equal to unity. Then, since $\varepsilon_1 - \varepsilon_2 \equiv |x|$, ($\varepsilon_1 \geq \varepsilon_2$, see Landahl, 1938), when S_1 and S_2 are replaced by S and S_s [equations (8) and (10)], h is a function of $|x|$, $h(|x|)$.

Since $\varepsilon_1 - \varepsilon_2 = |x|$ acts as a stimulus to the fibers leading to the center C , the amount of excitation at s_3 and s_4 due to C would increase directly as the expression $1 - e^{-a\theta|x|}$ [Rashevsky, 1938, Ch. XXII, equation (5)]. If h_0 is the initial threshold and I , θ , and α are constants, then

$$h = h_0 - \frac{A' I}{a' \theta} (1 - e^{-a\theta|x|}) , \quad (23)$$

or if h tends toward zero for large $|x|$, then

$$h = h_0 e^{-a\theta|x|} . \quad (24)$$

Now $h(x)$ may be determined in the following manner. From equations (6) or (14) we have

$$P'_d = \int_{(x-h)}^{(x+h)} p d(\varepsilon - j)' .$$

Differentiating with respect to x we have

$$\frac{d P'_d}{d x} = p(x+h) \cdot \frac{d}{d x} (x+h) - p(x-h) \cdot \frac{d}{d x} (x-h) . \quad (25)$$

Expanding, we obtain

$$\begin{aligned} \frac{d P'_d}{d x} &= \left[p(x) + h p'(x) + \frac{h^2}{2} p''(x) + \dots \right] \left[1 + \frac{d h}{d x} \right] \\ &\quad - \left[p(x) - h p'(x) + \frac{h^2}{2} p''(x) + \dots \right] \left[1 - \frac{d h}{d x} \right] \\ &= 2 h p'(x) + 2 p(x) \frac{d h}{d x} + h^2 p''(x) \frac{d h}{d x} + \dots . \end{aligned} \quad (26)$$

Integrating, we have

$$\begin{aligned} P'_d &= 2 h p(x) + \int h^2 p''(x) d h + \dots \\ &= 2 h p(x) + \frac{h^3 p''(x)}{3} + \dots + \dots . \end{aligned} \quad (27)$$

Solving for $h(x)$ we have

$$h(x) = \frac{P'_d}{2 p(x)} - \frac{h^3(x) p''(x)}{6 p(x)} + \dots, \quad (28)$$

where the second term on the right is a correction term which gives an estimate of the error made in the approximation. Since P'_d and $p(x)$ may be determined empirically, $h(x)$ may be obtained. In the inset of Figure 1 the $h(x)$ relation is shown for lifted weights, h and x being both given arbitrarily in units of grams. In this case, h and x are essentially independent. The correction indicated by the second term on the right hand side of equation (28) was made. The maximum correction was 0.10 grams or 5%, and the mean absolute correction was 0.05 grams or 2.7%. The next higher order corrections are much smaller and negligible.

In order to determine $p(x)$ in equation (28) the following method was used instead of the more direct but less reliable method of measuring the slopes of the empirical $P(x)$ relation. Since the $P(x)$ relations are so nearly Gaussian, the assumption of normality may be made and hence, for a given x , $p(x)$ is determined, as is also $p''(x)$. Actually, the $P_g = P(x)$ value is here given equal weight with the average of the other two points for each x , P'_g and $(1-P'_l)$. If this is done, a graphic average is necessary, as otherwise the result will be systematically increased when the P values are less than 50 per cent, and decreased when greater. As an example, the numerical average between 1 and 9 per cent is 5 per cent as compared with the graphical average of 3.3 per cent.

If h is not independent of x , plotting P'_g , P_g , and $P'_g + P'_d$ on arithmetic probability paper will not result in three parallel lines. In Figures 2 and 3 are shown averaged results of visual and auditory data by W. N. Kellogg (1930) and in neither case can three parallel lines (or even curves with parallel tangents at each point) very well approximate the data. In both these sets of data, the two category and three category cases were presented separately. Each of five subjects made 288 judgments on two sets, each set including both the two and the three category method. In the averages given in the figures not all sets could be included as the intervals were not uniform. For the visual data represented, each point was based on 720 judgments while for the auditory data each point was based on 1152 judgments.

As may be seen in Figures 2 and 3 the $h(x)$ relation is not constant. In the insets of the figures are plotted the relation as derived from the data by means of equation (28). The correction term was taken into account as in the case of the lifted weights. The order of magnitude of the correction term in per cent was the same in the

three cases. As in the lifted weight data, the results for individual cases in both the light and the sound experiments were distinctly like that of the respective averages shown in the figures.

In order to fit the curves for the visual data (Kellogg, 1930) it was assumed that $h(x)$ was given by the derived equation (24). The curve in the inset of Figure 2 was obtained from (24) by plotting the logarithm of h against x and determining the slope and ordinate intercept of a straight line drawn through the points, thus obtaining $h_0 = 0.49$ meter candles and $\alpha \theta = 1.14$ meter candles⁻¹. In each of the cases x is measured from the mean, 0.10 meter candles. The three curves in Figure 2 were obtained as follows. The central straight line, (P_g), represents a normal cumulative curve having a standard deviation, σ , of 0.58 meter candles and with the mean, x_0 , at 0.10 meter candles the line should pass through the solid circles. The upper and lower curves were obtained respectively from equations (15) and (13) with the appropriate values of h given by equation (24) and with the constants given above. The curves should pass through the open circles and crosses respectively. The x values were again measured from the mean. The standard intensity was 21.68 meter candles.

The ordinates in Figure 2 are differences between the standard and the comparison stimuli in meter candles. We are justified in using such a scale since $|S - S_s| \ll S_s$ and the approximate relation in (10) holds accurately. However, the particular ordinate scale used in this case is due to the experimental procedure employed. The subjects were asked to respond "left" or "right" according as they judged the left or right stimulus to be the darker. In our notation, P_l represents the proportion of judgments "left" and P_g represents the proportion of judgments "right". The sign of the ordinate is then rather arbitrary. In the figure a positive difference means that the stimulus to the left is the darker. The constant error was such that, for equal stimuli, the one to the left was judged the darker.

In the derivation of equation (24) the threshold of the fibers exciting the center C was neglected. Had this not been done, the curve in the inset of Figure 2 would have had a flat top to a distance, on either side of the mean, corresponding to the threshold neglected. The curve would then continue as shown. However it should be recalled that the same randomness present at the discrimination center would also be superimposed on the $h(x)$ relation derived in equations (23) and (24). The effect would be to round off any discontinuities otherwise present. The resulting trend is illustrated in the figures by broken lines (Figure 2).

In the experiment on sound stimuli (Kellogg, 1930), the sub-

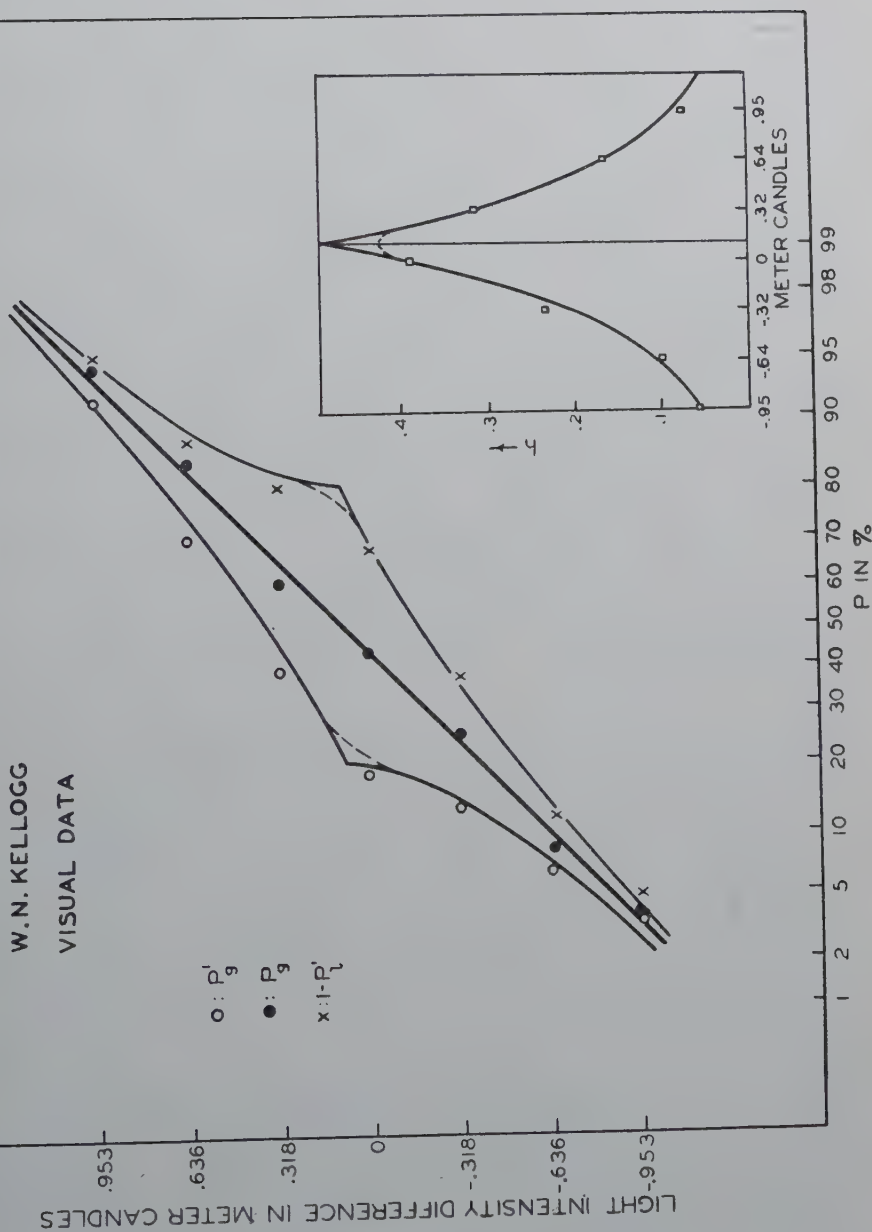


FIGURE 2

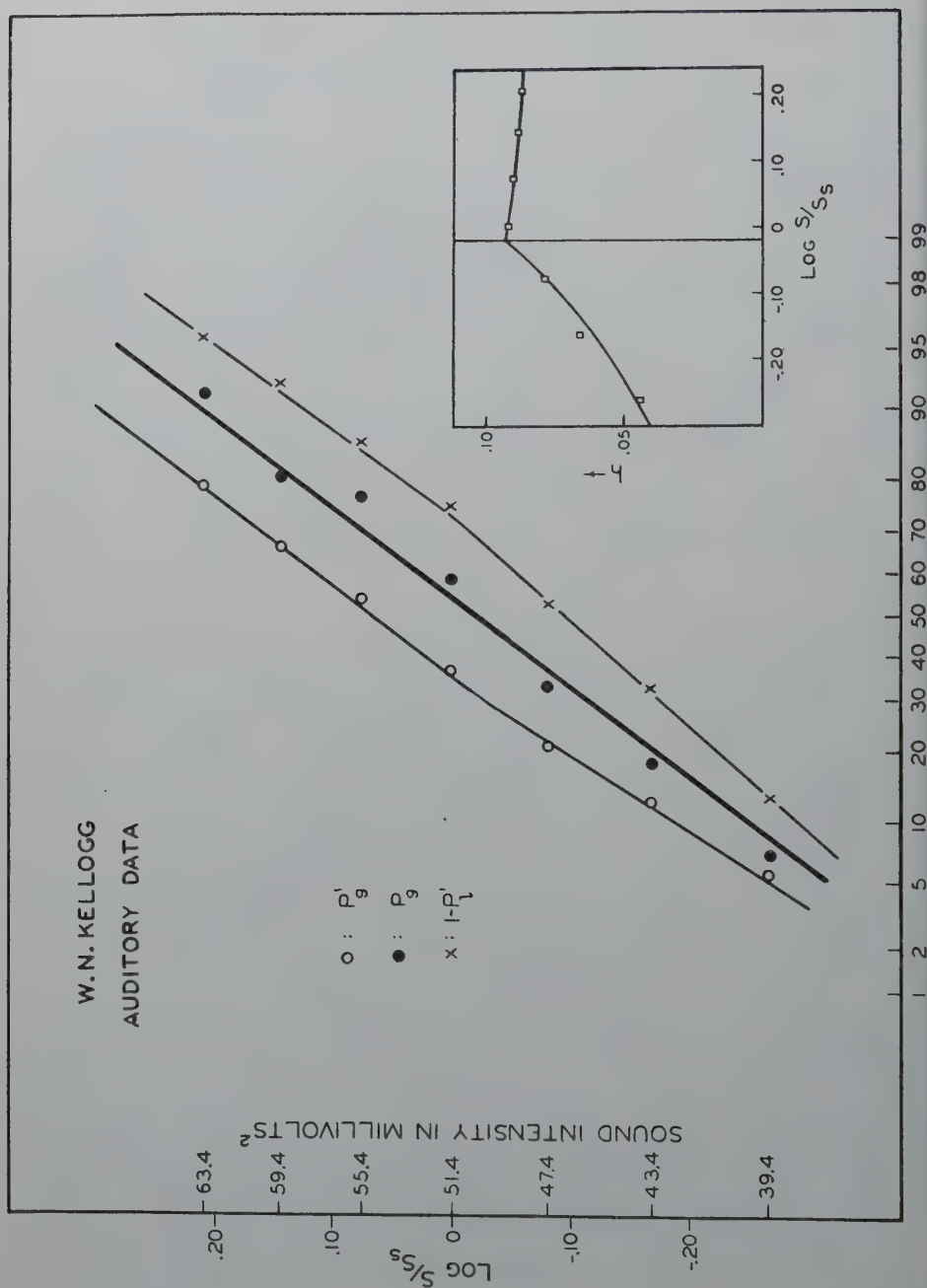


FIGURE 3

ject was asked to report "stronger" or "weaker" according as he judged the comparison stimulus to be stronger or weaker than the standard. Since in this case $S - S_s$ may be almost one-fourth of the value of S_s the linear approximation in (10) cannot be used as the approximation breaks down rapidly when the difference is much over ten per cent. When a linear ordinate is used, the graph corresponding to Figure 3 shows an average trend which is noticeably concave upwards. The use of the more exact logarithmic ordinate as in Figure 3, and in accordance with equation (10), makes it possible to obtain excellent agreement with the theoretically derived relations. The outside scale is the natural logarithmic scale. The inner values are the sound intensities expressed directly in (millivolts)².

The $h(x)$ relation in the case of the auditory data, plotted in the inset of Figure 3, is definitely asymmetrical. In order to fit the data it is necessary to allow for the asymmetry by introducing two values for the parameter $\alpha\theta$ of equation (24). For $S > S_s$ or $x > 0$, $\alpha\theta$ is taken as 0.35 ordinate units while for $S < S_s$ or $x < 0$, $\alpha\theta = 2.8$. Also $h_0 = 0.93$ in terms of the ordinate units or approximately 5 (millivolts)². The distribution is assumed normal and the standard deviation, σ , is taken as 0.18 or approximately 9 (millivolts)². The three curves in Figure 3 are then obtained from equations (15), (12) and (13) in which h is given by equation (24), with the parameters as given above.

From Figure 3 it may be noted that there is some evidence that the standard deviation of the data from the two category method is smaller than that of the three category (Kellogg, 1930, p. 43).

From a comparison of the $h(x)$ relations plotted in the insets of Figures 1, 2 and 3, one is lead to conclude that the form of the relations in each case is perhaps significantly distinct, especially since the individual cases resemble their respective averages. Let us suppose that they are in fact distinct and that this result is not due to a chance grouping of the 17 subjects involved.* The differences may then be due to the modalities involved or to the experimental procedures or both. From the brief description of the experimental procedures given above it is clear that the procedure for the lifted weight experiment was distinctly different from that for the sound or light experiments. In an experiment on lifted weights by E. Culler (1926) with himself as subject and with the same procedure followed as that of F. M. Urban (1908), there is an indication that h might decrease

* Four of these subjects could not be included in the averages under discussion for reasons explained above. Though the number judgments for the individual cases is not too large, 144 to 450, the trend of the $h(x)$ relation empirically derived is very stable, especially in the visual and lifted weight data.

with $|x|$. But in the experiment by J. P. Guilford (1936) on one subject, with constant errors experimentally eliminated and with the two and the three category cases separately presented, there is rather distinct indication of an $h(x)$ relation similar to that of the visual data. The experimental points are in this case rather scattered. There is a suggestion, however, that the mode of presentation is of importance in this particular respect. If this suggestion should prove to be correct, it will require a natural explanation on the basis of the mechanism.

For each of the five subjects in the visual experiment the values of σ , h_0 and $\alpha \theta$ of equations (22) and (24) were obtained in the units used above. Between h_0 and $\alpha \theta$ a correlation of 0.1 was found. The correlation between h_0 and σ was 0.9, and between $\alpha \theta$ and σ , 0.2. These correlations and others, though not reliable, do impose restrictions on the mechanism under discussion and they must be satisfied. For the present we shall not attempt to interpret these not too reliable results.

In Figure 2 it is clear that the three category data do not lie along two straight lines. The question then arises as to the meaning of the standard deviation unless, as above, a variable h is introduced. If the mean slope is taken, the value obtained will vary with the range. Evidently a numerical determination of the standard deviation is no longer satisfactory since the initial assumption of normality is not too good. This is particularly the case in determining the critical ratio of a difference. Two curves which are clearly different may have a negligible critical ratio, and conversely, two curves having the same mean slope (on probability paper) may show a fairly large critical ratio obtained numerically.

In this section the results obtained in the previous section are compared with experimental data. Certain revisions in the initial assumptions were necessary in order to obtain agreement with the data. The purpose has been to illustrate the results obtained, to demonstrate the method of determining the parameters and to interpret on the basis of the mechanism the meaning of any significant lack of agreement with experimental data.

III

Let us now attempt to apply results previously obtained to the *Wahlmethode* of Fechner. Consider again a structure similar to that of Figure 1 (Landahl, 1938) but having n first order fibers instead of two, and each first order fiber exciting $n-1$ inhibitory fibers so that there are $n(n-1)$ inhibitory fibers instead of 2. Let n stimuli be presented simultaneously and let the stimulus magnitudes S_i be

unknown but be so ordered that $S_i > S_j$ for $i < j$. If P_{i1} is the probability that a response is made to S_i as the largest stimulus when all n stimuli are presented and if P_{ci1} is the corresponding probability corrected for chance, then

$$P_{ci1} = \frac{n}{n-1} \left(P_{i1} - \frac{1}{n} \right). \quad (29)$$

From equation (46) of the previous development (Landahl, 1938), we have in the above notation

$$P_{ci1} = \frac{L \xi}{n-1} \log \frac{S_1^{n-1}}{S_2 S_3 \cdots S_n}, \quad (30)$$

where L is defined by equation (9) and ξ corresponds with the reciprocal of σ^2 of equation (22). We shall assume ξ to be independent of n .* P_{ci1} is the probability corrected for chance that the largest stimulus S_1 is responded to as the largest. Then from equations (29) and (30) we may write

$$P_{i1} = \frac{1}{n} + \frac{L \xi}{n} \log \frac{S_1^{n-1}}{S_2 \cdots S_n}. \quad (31)$$

Now define z_i by

$$z_i = L \xi \log \frac{S_i}{S_0}, \quad (32)$$

where S_0 is an arbitrary value. Comparing equation (32) with (10) we see that x is proportional to z_i for $S = S_i$ and $S_s = S_0$. Equation (31) then becomes

$$P_{i1} = \frac{1}{n} + z_1 - \frac{1}{n} \sum_{k=1}^n z_k. \quad (33)$$

Now let S_1 be removed and the remaining $n-1$ stimuli be presented. Then in place of equation (33) we may write

$$P_{22} = \frac{1}{n-1} + z_2 - \frac{1}{n-1} \sum_{k=2}^n z_k, \quad (34)$$

or more generally

$$P_{ii} = \frac{1}{n-i+1} + z_i - \frac{1}{n-i+1} \sum_{k=i}^n z_k. \quad (35)$$

* In the previous paper (Landahl, 1938), compare ξ in equation (46) with k (Landahl, 1938, p. 110) in equations (57), (58), and (18) and also with the expansion of equation (19) together with (20) and (18).

The probability P_{21} that S_2 is responded to as the largest, when there are n stimuli, is less than the probability P_{22} that S_2 is responded to when the largest stimulus S_1 is removed and S_2 is the largest of those left. Let us assume that the former, P_{21} , is equal to the latter, P_{22} , reduced by the factor $(1 - P_{11})$, or that the relative values remain unchanged, so that

$$P_{21} = (1 - P_{11})P_{22} \quad (36)$$

and more generally

$$P_{ij} = (1 - P_{jj})P_{i(j+1)}. \quad (37)$$

From equation (37) we have

$$P_{i1} = (1 - P_{11})(1 - P_{22}) \cdots (1 - P_{(i-1)(i-1)})P_{ii}, \quad (38)$$

which in turn may be written because of equation (37),

$$P_{i1} = (1 - P_{11} - P_{21} - \cdots - P_{(i-1)1})P_{ii}. \quad (39)$$

Substituting from equation (35), the above equation may be written, if we define

$$\Sigma_1 = \sum_{k=1}^n z_k, \quad \Sigma_j = \sum_{k=j}^n z_k, \quad (40)$$

$$P_{i1} = (1 - P_{11} - \cdots - P_{(i-1)1}) \frac{1}{n - i + 1} \times \left[1 + \sum_{k=1}^{i-1} z_k + (n - i + 1) z_i - \Sigma_1 \right]. \quad (41)$$

From equation (41) we have $n-1$ equations in n unknowns, z_i , since the n -th equation reduces to an identity

$$P_{n1} = (1 - P_{11} - \cdots - P_{(n-1)1}) \frac{1}{1} (1 + \Sigma_1 - z_n + z_n - \Sigma_1).$$

Therefore introducing

$$y_{i1} = z_i - \frac{\Sigma_1}{n} \quad (42)$$

or

$$y_{ij} = z_i - \frac{\Sigma_j}{n - j + 1}, \quad (43)$$

so that

$$\sum_{i=j}^{i=n} y_{ij} = 0, \quad (44)$$

we have for equation (41),

$$y_{i1} = \frac{P_{i1}}{(1 - P_{11} - \dots - P_{(i-1)1})} - \frac{1}{n - i + 1} \left(\sum_{k=1}^{i-1} y_{k1} + 1 \right), \quad (45)$$

or because of equation (39), we may also write

$$y_{i1} = P_{ii} - \frac{1}{n - i + 1} \left(\sum_{k=1}^{i-1} y_{k1} + 1 \right). \quad (46)$$

If the n stimuli are presented and the proportion of responses that S_i is the largest is obtained for each i , or what is equivalent, P_{i1} , then the values of y_{i1} are given by successive substitutions in the equations represented by (45). Or if choices are made with the n stimuli present giving among other values P_{11} , then the most frequently chosen stimulus, S_1 , is removed so that the next group of choices determines P_{22} , etc., the values y_{i1} , may be most readily obtained from the equations represented by (46). For a given value of $L \xi$, the values of S_i are given by equation (32) if the values of z_i are known. Or if ξ is known and also the values of z_i , we may obtain x values. From equation (42) the values of z_i are seen to be the same as the values of y_{i1} , but displaced by an unknown amount \sum_1/n , a value which depends upon the stimuli used. The origin of measurement of z_i is then not determined without other information.

It should be noted that the equations do not imply that $y_{i1} > y_{(i+1)1}$ if $P_{i1} > P_{(i+1)1}$ or the converse. The possibility of inversions arises because it is assumed that the relative distribution of responses with and without the largest stimulus is the same in the derivation of equation (37). A stimulus for which the corresponding value of y_{i1} is inverted would then be expected to be most associated with the stimulus just larger or smaller than itself. The presence of a particular stimulus, then, not only changes the z_i or y_{i1} values uniformly but may do so non-uniformly.

We have assumed that ξ is independent of n . Depending on the details of the mechanism other relations may hold. If ξ is found to be independent of n , the use of the above procedure would be justified. However, its use would be restricted to the purpose of obtaining an additional relation among the parameters and effect of stimuli upon each other. The procedure suggested by J. P. Guilford (1937) leads to essentially the same results as that of the first section, as far as the evaluation of parameters is concerned.

On applying certain results previously obtained to the method of choices it is found that only one restriction can be imposed upon the parameters; that the scale values derived may not be correctly ordered, and will generally be displaced by an unknown amount; and that the absolute unit will not be obtainable.

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STREAMING IN DIFFUSION FIELDS

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Two simple systems are discussed in which diffusion of a dissolved substance causes continued circulation of the solvent, thru the mediation of gravitational forces in one case, and of solute viscosity forces in the other. The first is analagous to the circulation in a liquid heated from below.

Living cells frequently exhibit a steady streaming of their protoplasm. This phenomena has been the subject of considerable observation and experimentation, but there is as yet no satisfactory theory of the mechanism involved. Any such motion may be regarded as the result of driving forces operating against the viscous resistance of the protoplasmic substance, but the nature of the driving forces is not known. They appear to be intimately connected with the cell metabolism, and one suggestion is to look for their source in the process of diffusion, as has proven quite promising in studying the mechanics of cell division.

With these considerations in mind we shall discuss some cases of solvent motion in a diffusion field.

I

Consider a pair of vertical tubes of length L connected to form a loop and filled with a solution. Suppose the concentration of the dissolved substance to be maintained constant at the top and at the bottom of the loop, the values of the concentration being c'' and c' respectively, so that there is continual diffusion along the columns of solution. For simplicity we shall regard the tubes as one dimensional systems and deal only with average densities, velocities, pressures, forces, etc., over a cross section. The distance x will be measured upward from the bottom, capital and small letters will refer respectively to solvent and solute, the velocities V and v will be positive upwards, and the two tubes will be distinguished by subscripts 1 and 2, number 1 being chosen as the tube where the solvent is flowing upwards.

The gravitational pressure acting downward upon the solvent column in a tube is

$$g \int_0^L C \, dx, \quad (1)$$

g denoting the gravitational constant and C the concentration, while the diffusion drag acting upward is

$$p' - p'' - g \int_0^L c \, dx, \quad (2)$$

where p'' and p' are the solute pressures at top and bottom. The total pressure tending to make the solvent circulate up on side No. 1 and down on side No. 2 is therefore

$$J = g \int_0^L (C_2 - C_1 + c_2 - c_1) \, dx, \quad (3)$$

since p' and p'' are the same for both tubes and hence drop out in the subtraction. The quantity J is the driving force which acts against the viscous resistance of the solvent.

The flow must be the same across any cross-section, hence we have the equations of continuity

$$CV = K, \quad (4)$$

$$cv = k,$$

where K and k are constants. The solvent flow (unlike that of the solute) will be equal and opposite in the two tubes,

$$K = K_1 = -K_2; \quad (5)$$

and the viscous resistance to flow in a tube is proportional to the rate of flow. Thus, equating the driving force to the resistance,

$$J = \Theta LK \quad (6)$$

where Θ embodies the solvent viscosity and the cross sections of the tubes.

In general a solvent expands slightly when a solute is added and its density is correspondingly decreased. For dilute solutions this may be adequately represented by the linear relation

$$C = C_0 - bc, \quad (7)$$

where b is a constant and C_0 is the density of the pure solvent. Expression (3) then reduces to

$$J = g(1 - b) \int_0^L (c_2 - c_1) \, dx. \quad (8)$$

It remains to find the solute distribution in the two columns. Obviously if the solvent is at rest the situations will be identical, we shall have $c_1 = c_2$, and there will be no driving force. If, however, there is circulation of the solvent, then $c_1 \neq c_2$ and J may be different from zero and such as to maintain the circulation. This is related to work of Griffiths (1898, 1915).

Assuming (Young, 1938) a drag force between solvent and solute proportional to the product of their densities and their relative velocities, the solute pressure equation is

$$\frac{dp}{dx} = -gc - fcC(v - V); \quad (9)$$

which, introducing (4) and (7), and the Van't Hoff relation

$$p = \alpha c \quad (10)$$

$$\alpha = \frac{RT}{M},$$

becomes

$$\frac{dc}{dx} = A + Bc; \quad (11)$$

wherein

$$A = -\frac{fkC_0}{\alpha}, \quad (12)$$

$$B = \frac{fK + fbk - g}{\alpha}.$$

This has the solution

$$A + Bc = Ge^{Bx}, \quad (13)$$

where G is the integration constant. The boundary conditions $c = c'$ at $x = 0$, $c = c''$ at $x = L$ give

$$A + Bc' = G \quad (14)$$

$$A + Bc'' = Ge^{BL};$$

from which

$$A = B \frac{c' e^{BL} - c''}{1 - e^{BL}}, \quad (15)$$

this being essentially a relation between K and k expressing the fact that the rate of flow of the solute depends upon that of the solvent, as is apparent physically. From the above relations it follows that

$$c - c'' = (c' - c'') \frac{e^{Bx} - e^{BL}}{1 - e^{BL}}, \quad (16)$$

and

$$\int_0^L (c - c'') dx = -(c' - c'') L \left[\frac{1}{BL} + \frac{e^{BL}}{1 - e^{BL}} \right]. \quad (17)$$

The bracketed expression in (17) is a monotonic decreasing function of BL , as may be seen by considering

$$\phi(y) = \frac{1}{y} + \frac{e^y}{1 - e^y}.$$

We find $\phi(-\infty) = 0$, $\phi(\infty) = -1$. The derivative function

$$\frac{d\phi}{dy} = \frac{y^2 e^y - (e^y - 1)^2}{y^2 (e^y - 1)^2}$$

does not vanish at $y = 0$, and any other root would require a non-zero solution of $y/2 = \pm \sinh(y/2)$ which is impossible. Hence $d\phi/dy$ is everywhere negative.

Expression (8) may be written as

$$J = g(1 - b)(c' - c'') L [\phi(B_1 L) - \phi(B_2 L)]. \quad (18)$$

Now tube No. 1 has been chosen as the one in which the solvent moves upward, so that $K_1 = -K_2$ is positive. The solute flow will be greater on the side where it moves with the solvent, and, whichever the sign of $c' - c''$, we shall have $k_1 > k_2$. Then from (12) it is seen that $B_1 > B_2$, and hence $\phi(B_1 L) < \phi(B_2 L)$. Hence J is opposite in sign to $c' - c''$, and since J must be positive in (6) it follows that c'' must be greater than c' for the driving force to be in the right direction to tend to maintain the motion. Thus *the solute must be diffusing downward for steady solvent circulation to be maintained*. The solution is then less dense at the bottom, and the phenomena is analagous to circulation in a liquid heated from below, and the results and methods of this latter problem are of service in the diffusion case (Rayleigh, 1916; Jeffreys, 1926; Low, 1929; Hales, 1935; Schmidt, 1935, 1937). The case of time variable diffusion along a moving column has been treated by Somers (1912).

It is apparent that the system is in equilibrium when the solvent is at rest, for then the solute distribution is identical in the two columns. It will be shown, however, that *the system is unstable if the solvent is stationary and the concentration gradient $c'' - c'$ is sufficiently large*.

In (12) k is a rather complicated function of K , but since the so-

lute flow will be aided by increased convection in the same direction it is seen that k_1 increases monotonically with K_1 , while k_2 decreases monotonically. Hence as V increases from zero, B_1 increases and B_2 decreases so that J is monotonic with K . If dJ/dK at $K = 0$ is greater than ΘL of (6), then any small circulation will tend to increase and the state of zero circulation is unstable.

Neglecting the second term in the numerator of (12) we have $dB_1/dK = -dB_2/dK = f/\alpha$, so that from (18) at $K = 0$

$$\frac{dJ}{dK} \geq g(1-b)(c' - c'') \frac{2fL^2}{\alpha} \phi_0' \quad (19)$$

where ϕ_0' is the value of $d\phi/dy$ at y_0 corresponding to $K = 0$. The inequality sign enters because the term neglected in (12) would increase the value of dJ/dK . At $x = 0$ we find by series expansion that $\phi' = -1/12$; ϕ_0' will be of this order of magnitude. Thus the state of zero solvent circulation will be unstable if

$$(c'' - c') L > \frac{\alpha \Theta}{2fg(1-b)(-\phi_0')} \quad (20)$$

Estimating ϕ_0' to be $-1/12$ this is approximately

$$(c'' - c') L > \frac{6\alpha\Theta}{fg(1-b)} \quad (21)$$

The lowest stable circulation rate may be estimated by expanding ϕ by means of the Bernoulli series, convergent for $0 < x^2 < 4\pi^2$,

$$\frac{1}{e^x - 1} = \frac{1}{x} - \frac{1}{2} + \frac{x}{12} - \frac{x^3}{30.24} + \dots \quad (22)$$

Expression (18) then becomes

$$J = g(1-b)(c' - c'') \frac{L^2}{12} \left[-(B_1 - B_2) + \frac{(B_1^3 - B_2^3)L^2}{60} + \dots \right] \quad (23)$$

or, neglecting the b term in (12),

$$J = g(1-b)(c' - c'') \frac{L^2 f}{6\alpha} K \left[-1 + \frac{L^2}{60} \left(\frac{f^2 K^2}{\alpha^2} + 3 \frac{g^2}{\alpha^2} \right) \dots \right] \quad (24)$$

Equating this to ΘLK and removing the root $K = 0$ gives

$$K^2 = \frac{60\alpha^2}{f^2 L^2} \left[1 - \frac{g^2 L^2}{20\alpha^2} - \frac{6\alpha\Theta}{g(1-b)Lf(c'' - c')} \right] \quad (25)$$

as the approximate equation for the lowest stable circulation rate.

As $c'' - c'$ increases this expression tends to a limiting value

which, with g/α neglected, is

$$K = \pm 7.7 \frac{\alpha}{fL}. \quad (26)$$

Now f is proportional to T/D , where D is the ordinary Fick diffusion coefficient and T is the temperature, so that with α as given by (10) it is seen that (26) varies as D/ML , M being the molecular weight of the solute.

II

We now consider a system in which the solvent driving force arises not from gravity but from the viscosity of the solute. Suppose the tubes of the circuit to contain some sort of porous structure rigidly attached to the walls and thru which the solvent and solute have to move, such as a grid or network or a sponge structure. This gives a backward drag opposing the solute motion which will be assumed proportional to the total rate of solute flow, namely θLk per column where θ includes the solute viscosity and a structural factor. Instead of (3) and (8) we now have

$$J = L(\theta_2 k_2 - \theta_1 k_1); \quad (27)$$

while (9) changes to

$$\frac{dp}{dx} = -fcC(v - V) - \theta cv. \quad (28)$$

This is the same as (11) except that now

$$A = -\frac{k}{\alpha}(\theta + fC_0). \quad (29)$$

$$B = \frac{f}{\alpha}(K + bk).$$

As before, k is a rather complicated function of K , but k_1 increases monotonically with K_1 while k_2 decreases. Hence if $\theta_1 = \theta_2$ in (27) it is seen that the driving force always opposes the motion. Hence *solvent circulation is possible only if the tubes have different structure resistance factors.*

Expression (15) may be written as

$$A = B \left[\frac{c' - c''}{1 - e^{BL}} - c' \right]; \quad (30)$$

and with (22) this becomes

$$A = B \left[(c' - c'') \left(-\frac{1}{BL} - \frac{BL}{12} + \dots \right) - \frac{c' + c''}{2} \right], \quad (31)$$

or

$$A = (c' - c'') \left(-\frac{1}{L} - \frac{B^2 L}{12} + \dots \right) - B \frac{c' + c''}{2}. \quad (32)$$

Neglecting θ in comparison with fC_0 in (29) we have from (27)

$$J = \frac{\alpha L}{fC_0} (A_1 \theta_1 - A_2 \theta_2), \quad (33)$$

and with (32) and (29) we find, to the first power of B in (32),

$$J = \frac{\alpha}{fC_0} (c' - c'') (\theta_2 - \theta_1) - \frac{L}{C_0} \frac{c' + c''}{2} \left[K(\theta_1 + \theta_2) + b(\theta_1 k_1 - \theta_2 k_2) \right]. \quad (34)$$

Noting that the last term in the bracket is proportional to J this gives

$$J \left(1 - \frac{b}{C_0} \frac{c' + c''}{2} \right) = \frac{\alpha}{fC_0} (c' - c'') (\theta_2 - \theta_1) - \frac{L}{2C_0} K (c' + c'') (\theta_1 + \theta_2). \quad (35)$$

Since $bc \ll C_0$ in (7) the left side is very nearly equal to J , and (6) then becomes

$$KL \left[\Theta + (\theta_1 + \theta_2) \frac{c' + c''}{2C_0} \right] = \frac{\alpha}{fC_0} (c' - c'') (\theta_2 - \theta_1) \quad (36)$$

The left side is approximately $KL \Theta$, and thus

$$K = \frac{\alpha}{\Theta L f C_0} (\theta_2 - \theta_1) (c' - c''). \quad (37)$$

The signs are such that *the solvent flows in the same direction as the solute in the tube where the structure is more porous*. The speed is proportional to

$$\frac{D}{\Theta} \frac{\theta}{M} \frac{1}{L} \frac{c' - c''}{L}. \quad (38)$$

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ERRATA

In the paper "The Mechanism of Cell Division" by N. Rashevsky, pp. 23-30, the following somewhat confusing notation should be changed: substitute I for T in last term of equation (1); in left hand side of equation (3); in first line from top on page 25; in 12th and 19th line from top on page 27; in left hand side of equation (20).

In formula on 10th line from bottom on page 24 the expression in braces should be multiplied by c .

In the paper "On the Mechanics of Viscous Bodies and Elongation in Ellipsoidal Cells" by Gale Young, pp. 31-46, replace V by v on page 31 last line; page 32, equation 4; page 33, lines 4 and 5. In equations (6) and (9) replace η by n in arguments of the cosine function, pages 32-33. Also in equation (13). n denotes direction of normal to surface. Change ϕ to Φ in equation (32) and 6th line from bottom of page 37. Replace n by η on right side of (63).

In the paper by Gale Young, "Elongation and Constriction in Cell Division," pp. 75-91, in equation (36) page 85, replace $(\cos nz)$ by $\cos(nz)$. Change v to V in equation (43) page 86.

In the paper by N. Rashevsky, "Mathematical Biophysics of Growth," pp. 119-127, in equation (26) page 123, the coefficient of the log term should be $3/2$.

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